RESTING STATE FUNCTIONAL CONNECTIVITY AND CONSCIENTIOUSNESS

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Abstract

Of the Big Five personality traits, Conscientiousness is most closely associated with individual differences in goal attainment, but little is known about its neural basis. Broad neural networks can be studied in fMRI using functional connectivity, which identifies brain regions that act in synchrony. We tested the novel hypothesis that a network resembling the salience and ventral attention networks may be one of the main neural substrates of Conscientiousness. Self- and peer-ratings of Conscientiousness were collected in a community sample of adults (N = 218) who underwent a resting-state fMRI scan. An independent component analysis was conducted identifying four subcomponents of a network we named the goal priority network (GPN). We examined coherence within and between these GPN subcomponents, and results indicate that coherence in one of the components, comprising insula and dorsal anterior cingulate cortex (dACC), is significantly associated with Conscientiousness. Connectivity between this insula/dACC component and the three other GPN components was also significantly correlated with Conscientiousness. Our results support the hypothesis that variation in salience and ventral attention-like networks may be central to trait Conscientiousness, and that these networks may be components of one overarching goal maintenance network.

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Resting State Functional Connectivity and Conscientiousness

Personality traits are relatively stable individual differences that impact various life outcomes. Better health is associated with more satisfaction in life (Strine, Chapman, Balluz, Moriarty, & Mokdad, 2008), and Conscientiousness is the Big Five trait most closely associated with healthy habits (Ozer & Benet-Martínez, 2006; Roberts, Lejuez, Krueger, Richards, & Hill, 2014). Unhealthy habits, such as smoking, improper diet, and lack of exercise, are negatively correlated with Conscientiousness. Higher trait Conscientiousness has been shown to be related to lower instances of substance abuse, better intergenerational and familial relationships, satisfaction in dating couples, better job performance, and higher grade point averages among students. Most of these associations with Conscientiousness make sense; it is the Big Five trait most linked to pursuing long-term goals while avoiding distractions and inhibiting disruptive impulses (DeYoung et al., 2010). Nonetheless, the specific cognitive operations that subserve these functions are not well understood.

One likely candidate for a cognitive operation central to Conscientiousness is successfully prioritizing the steps involved in complex goal-pursuit. Stock and Beste (2015) found that Conscientiousness selectively predicted successful multicomponent behavior involved in completing a task that required flexible adjustment of the priority of multiple response steps and that Conscientiousness accounted for 19% of the inter-individual variance. Individuals higher in Conscientiousness were both more efficient in situations that required simultaneous engagement in multiple cognitive domains and also more effective at serial processing techniques to achieve a goal. Lastly, they found no

associations between other Big Five traits (Neuroticism, Openness/Intellect, Extraversion, and Agreeableness) with multicomponent efficiency and efficacy.

Hypotheses about cognitive operations can inform hypotheses about neural processes. Relatively few studies have examined the neural underpinnings of Conscientiousness (Allen & DeYoung, 2016). Much of the previous research on neural underpinnings on personality has focused on Extraversion and Neuroticism because of their links to psychopathology and basic processes of reward and punishment. The aim of this paper is to investigate the neurobiological underpinnings of Conscientiousness based on a recently developed hypothesis (Allen & DeYoung, 2016; DeYoung, 2015).

The neurobiological underpinnings of Conscientiousness are not well understood. Personality neuroscience is challenging because many brain regions are involved in a multitude of functions, and the potential neural mechanisms of Conscientiousness are currently less clear than for other Big Five traits. The lateral prefrontal cortex (LPFC) is an obvious potential candidate related to Conscientiousness because it is involved in rule-following and successful goal-maintenance (Bunge & Zelazo, 2006, Paxton, Barch, Racine, & Braver, 2008), and indeed studies have found that volume of regions in LPFC is positively correlated with Conscientiousness (DeYoung et al., 2010; Jackson et al., 2011; Kapogiannis et al., 2013; though see Bjørnebekk et al., 2013; Hu et al., 2011; Liu et al., 2013 for replication failures). However, the function most often associated with LPFC is working memory, which is unrelated to Conscientiousness (DeYoung et al., 2005, 2009, 2011). For example, previous studies have found that the LPFC, anterior cingulate cortex (ACC), superior parietal regions, and the medial frontal gyrus are all

related to working memory task performance and that activation of these regions can be observed while completing a working memory task in the scanner (Nee et al., 2013). Additionally, working memory is strongly correlated with IQ, and function and structure of the LPFC are also associated with IQ (Alloway & Alloway, 2010; Duncan et al., 2000; Kane & Engle, 2002). Given the relationship between working memory and IQ, it makes sense that previous research shows either a weak negative correlation between Conscientiousness (and closely related traits, like Grit, that can be described as facets of Conscientiousness) and IQ or no correlation between Conscientiousness and IQ at all (DeYoung, 2011; Duckworth et al., 2007; Higgins et al., 2007; Luciano et al., 2006). The search for neural underpinnings of Conscientiousness can be more targeted by understanding of the behavioral relation of IQ and working memory with Conscientiousness.

The fact that LPFC is associated primarily with working memory and intelligence, but that Conscientiousness is unrelated to these cognitive variables, raises a puzzle we believe may be resolved by the observation that multiple large-scale neural networks are present in LPFC. A recent study by Yeo and colleagues (2011) provided parcellated maps that were based on resting-state functional MRI scans of 1,000 healthy subjects, which is an impressive sample size for fMRI research. Their main findings suggest that there are seven main networks in the brain (which they labeled visual, somatosensory, dorsal attention, ventral attention, frontoparietal, limbic, and default). Most of the LPFC was included in the frontoparietal control network, which is most closely associated with IQ and working memory. However, the default and ventral attention networks also contain

regions of LPFC, albeit smaller ones. Therefore, three distinct networks appear to be present in the LPFC: the default network (DN), the frontoparietal control network (FPCN, also sometimes called the central executive network), and the ventral attention network (VAN). The DN shows increased activity in the absence of an externally oriented task (e.g., when individuals are engaging in self-directed thought or episodic memory recall) (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010, Sridharan, Levitin, & Menon, 2008). The FPCN has been proposed to play a role in goal-directed behavior, but previous research often finds associations between the FPCN and other cognitive tasks such as working memory (Menon & Uddin, 2010, Sridharan, Levitin, & Menon, 2008). The VAN or salience networks have been hypothesized to play the role of mediator between the DN and FPCN; that is, the VAN may function as one dynamic network that switches one's attention towards and away from goals depending on stimuli in the environment (Menon & Uddin, 2010). Allen and DeYoung (2016; DeYoung 2015) have recently hypothesized that the network Yeo and colleagues (2011) labeled the VAN is selectively related Conscientiousness.

Before laying out the specific evidence that led to this hypothesis, it is important to understand the relevance of whole brain resting state functional connectivity analyses to more traditional ways of thinking about brain function. Both structural and task-based fMRI may be used to constrain our hypotheses to specific areas or networks, either volumetrically or in terms of activations that are elicited during a task or at rest. While this is important for laying the groundwork for future studies, these methods do not tell us about individual differences in functioning on a broader, network level. Additionally,

studies on individual brain areas do not elucidate our questions about whole brain function, but most early studies with a focus on regions of interest provide us with a springboard for understanding how components of neural systems interact in large-scale networks. One way to study these interactions is by using functional connectivity methods.

Functional connectivity studies allow researchers to develop a network perspective of behavioral outcomes. Independent component analyses provide a way to identify core networks in the brain and also allow researchers to identify behavioral deficits associated with specific neural networks (Menon & Uddin, 2010). By gathering resting state fMRI data, researchers are able to look at the coherence of individual networks (i.e. how much synchrony in activation is present between voxels in a network) as well as inter-network functional connectivity (how synchronous one network is with other networks) or *interconnectivity*. This functional connectivity is based on "physiological coupling" that varies over time, which allows for a different kind of insight than simply looking at white matter structure, or regional activations (Menon & Uddin, 2010, p. 656). Individual networks studied using functional connectivity are referred to as intrinsic connectivity networks, or ICNs.

Functional connectivity ICNs can be obtained during both resting state and task-based fMRI. It might seem counter-intuitive that resting state fMRI results can be linked to a host of non-resting behaviors, but previous research shows that very similar networks are reliably measured and replicated at rest and during task-based fMRI. For example, performance on a working memory task was correlated with functional connectivity

during the working memory task but also functional connectivity at rest in the same network (Hampson, Driesen, Skudlarski, Gore, & Constable, 2006). This suggests that there are similar patterns of neural interaction present in both task-based activations as well as resting-state activations. ICNs are not likely to be exclusively associated with intentional cognitive processes because we find similar networks when assessing functional connectivity of people who are asleep or under anesthesia (Vaidya & Gordon, 2013). Connectivity between networks and coherence within networks varies between individuals, but similar networks are observed within the brain across individuals (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010). There are similar patterns of interconnectivity and coherence within networks during both task-based fMRI and resting-state fMRI. Thus, it is possible to observe a common core of networks in the brain across people. These common networks provide a platform to study variability in coherence or interconnectivity between individuals (Smith et al., 2009). Because brains have both modularity (localized information processing functions) and connectivity (these regions communicate to one another), task-free analysis of functional connectivity will help us figure out how functional (as opposed to structural) architecture supports aspects of human behavior (Seeley et al., 2007).

Functional connectivity and coherence allow researchers to study functional brain differences between individuals, and thus, it is possible to study traits in comparison to functional connectivity and coherence. Adlestein and colleagues (2011) observed that individual differences in personality corresponded to functional connectivity and coherence differences across individuals, even while the shapes and coverage of ICNs are

similar across individuals. Additionally, there are meaningful individual differences in patterns of connectivity among people who do not have neurological or psychiatric illnesses (Barch et al., 2013; Vaidya & Gordon, 2013). This is further evidence for a continuum of traits that are related to brain function which in turn are manifested as real-world behavioral differences between people. Thus, in the present study, functional connectivity analyses are used on resting state fMRI data.

There are many different ways to analyze functional connectivity data. It is important to note that using independent components analysis (ICA) functional connectivity methods are different from structural MRI and task-based fMRI functional connectivity methods (i.e. seed-based methods) and may highlight networks that would otherwise be overlooked. Structural MRI and task-based fMRI research is anatomically defined and proposed, but ICA functional connectivity analyses allows researchers to understand how the brain is organized and utilized within and between structural areas that may not be intuitive candidates for network analyses. For example, an event-related, task-based fMRI study found activation in regions that are now often called the salience network much earlier than ICA functional connectivity studies explored the same region (Clark, Fannon, Lai, Benson, & Bauer, 2000, Seeley et al., 2007). However, ICA functional connectivity studies tell us a bit more about how each of these regions in the salience network behaves synchronously. Task-based fMRI methods may be necessary to figure out what regions are engaged in specific task-based contexts, but thinking about them in terms of larger, distributed, persistent networks may be more useful for understanding how individual differences that influence behavior are manifested in the

brain. Previous literature utilizing task-based fMRI, structural MRI, and functional connectivity analyses allow for a targeted approach to identifying potential components and neural underpinnings of Conscientiousness.

The regions of LPFC that were linked to Conscientiousness by the studies mentioned above (DeYoung et al., 2010; Jackson et al., 2011; Kapogiannis et al., 2013) are all close to the regions of LPFC included in the VAN by Yeo and colleagues (2011). The VAN is a plausible neural substrate of Conscientiousness because areas of the VAN (e.g. the LPFC) are involved with planful behavior and are also involved with the ability to follow complex rules. Damage to the areas in the VAN, such as the DLPFC (Brodmann's area 9), has been shown to be associated with lower self-discipline (i.e. lower motivational stability) in traumatic brain injury patients compared to healthy controls (Forbes et al., 2014). These structural analyses allow researchers to investigate specific regions in comparison to traits, but do not directly measure brain function, which underlies behavior.

Task-based functional MRI has been used to evaluate Conscientiousness in the context of behavioral responses and has also found regions in the VAN to be related to Conscientiousness-like behaviors (e.g. inhibition, impulsivity, inhibitory control). Research has shown that there is reduced activity in the ventral prefrontal cortex (vPFC) as inhibition (effortful control to restrain impulses) decreases; that is, more impulsive behaviors are associated with decreased vPFC activity (Brown, Manuck, Flory & Hariri, 2006). Additionally, the DLPFC has been associated with impulsivity. The more behaviorally impulsive an individual behaved during a task-based fMRI, the less the

DLPFC activation (Asahi, Okamoto, Okada, Yamawaki, & Yokoto, 2004). Sampaio and colleagues (2013) reported that Conscientiousness was correlated with increased connectivity within the parietal cortex during a resting state scan; however, connectivity in the ACC was negatively correlated with the trait during resting state. Another study reported that the right inferior frontal gyrus (rIFG) showed increased activation at the same time as inhibitory control was elicited compared to baseline responding (Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010). Structural and functional MRI techniques find similar regions within the VAN to be involved with Conscientiousness (e.g., LPFC).

Whole brain functional connectivity research on Conscientiousness is generally lacking, but there have been a few studies investigating the relationship between neural connectivity and Conscientiousness. Adelstein and colleagues (2011) used resting-state functional connectivity to assess potential neural correlates of the Big Five personality traits. The researchers placed seed regions in cognitive "hubs" in the brain, the precuneus and ACC. Conscientiousness showed higher functional connectivity within the medial temporal lobe, which is involved with future-oriented judgments and planning. Higher Conscientiousness was also associated with higher functional connectivity between the medial temporal lobe and the ACC. This appears to contradict previous functional connectivity research by Sampaio and colleagues (2013) where functional connectivity within the ACC was negatively correlated with Conscientiousness. It is important to note that both of these studies had small samples (N = 39, N = 49, respectively), which may result in unreliable findings.

We attempted to develop a hypothesis about how large-scale functional connectivity networks may be related to Conscientiousness, based primarily on previous literature discussed by Allen and DeYoung (2016) and DeYoung (2015). The DN is most active while individuals are "at rest" or engaging in self-directed thought and the FPCN is most active during working memory and demanding cognitive tasks. Thus, it seems reasonable to postulate that the VAN and salience networks are the most likely networks contributing to long-term goal achievement and Conscientious behaviors. Sampaio and colleagues (2013) found that Conscientiousness did not correlate with any resting state activity in the DN, but that Neuroticism and Openness/Intellect were correlated to many DN ICNs. Since the FPCN is most closely associated with working memory or other cognitive tasks that correlate with IQ, it is unlikely to be the neural substrate of Conscientiousness given that trait's lack of relation with those constructs. Given the lack of relationship between Conscientiousness and both IQ and working memory, we propose that Conscientiousness will *not* be related to the neural network primarily implicated in working memory. Rather, Conscientiousness will be related to a different brain network (the VAN) that is implicated in goal maintenance and long-term goal achievement.

The VAN and salience network are generally discussed as two distinct but related networks. However, the VAN-like network identified by Yeo and colleagues (2011) appears to be a combination of networks that are traditionally referred to as the VAN and the salience network. We propose to call this larger network the goal priority network (GPN). Other researchers have focused more specifically on the VAN. Fox and colleagues (2006) reported that the VAN reorients attention in response to 'salient'

sensory stimuli. For example, the VAN is the part of the brain that assesses whether or not stimuli are important to the self. They also found that the VAN shows spontaneous activity during resting state MRI tasks, but that it is dissociable from the DN. Additionally, the ventral system reacts more strongly to task-relevant distractors than task irrelevant distractors, which may suggest that long-term goals are more central to the VAN and that there may be a different impulsivity or inhibition function elsewhere in the brain (Fox et al., 2006). The temporal parietal junction and the right ventral frontal cortex seem to be implicated in the VAN as proposed by Fox and colleagues (2006). Other researchers report that the salience network is most closely associated with the dorsal ACC and orbitofrontal cortex (Seeley et al., 2007). The right inferior frontal cortex (rIFC) is a critical region for recruiting inhibition, but the right anterior insula (rAI) also seems to play a role in inhibition (Ghahremani, Rastogi, & Lam, 2015). Previous studies also suggest that rAI may play a role in maintaining attention and focus during tasks at hand, but that the rIFC plays a role in inhibiting impulses. However, the findings of Yeo et al. (2011) suggest that all of these regions are part of the larger GPN. Inhibiting impulses, maintaining attention, and orienting attention towards stimuli are important to the self could all be considered parts of behaviors associated with motivational goal stability. Many of these networks and sub-regions of these networks are frequently studied separately or are referred to by different names, but due to their similar functions it makes sense that these systems all work together and comprise a bigger network. Thus, for the remainder of this paper, relevant ICNs in this analysis will be described as parts of the GPN.

The present study identified ICNs emerging from an ICA that appeared to correspond to parts of the GPN and tested their associations with Conscientiousness. We hypothesized that these ICNs would reflect individual differences in coherence and interconnectivity values systematically related to Conscientiousness. Also, these associations will be relatively specific, such that other Consciousness would not be associated with FPCN and DN ICNs, and other Big Five traits would not be associated with GPN ICNs. This is the first systematic analysis of Conscientiousness within the framework of resting state functional connectivity and identifies regions of the brain that are involved with motivational goal stability.

Methods

Participants

A healthy community sample *(N* = 306, age range: 20-39, all right handed) was collected as part of a study of neurobiological correlates of decision-making and personality. Participants were recruited via Craigslist and via fliers posted in public areas. A total of 218 participants were retained after assessing whether or not each subject qualified for the current analysis (51% female, mean age = 25.8 years). Exclusions were mostly due to MRI-related problems including: attrition (did not return for MRI scan, n=6), unusable or poor quality data (n=9), excessive movement during the scan (defined as average absolute displacement above 0.5mm or any single instance of X,Y, or Z coordinate displacement above 2.75mm, n=57), incomplete scanning sessions (n=11), and incomplete behavioral assessments (n=5). The current analysis utilized the same sample as Abram et al. (2015) with stringent motion parameters because these parameters

resulted in cleaner ICNs after running the ICA analysis and fewer ICNs identified as noise due to motion. Males and females did not differ significantly in terms of age, IQ, or ethnicity. Exclusion criteria were used in recruitment to exclude potential subjects who were diagnosed with neurological or psychiatric conditions, or if subjects were currently using psychotropic medications. Additional exclusionary criteria were used during recruitment for MRI safety reasons per the Center for Magnetic Resonance Imaging guidelines. Subjects were not excluded for alcohol or illicit drug use; however, if subjects endorsed current and substantial drug or alcohol dysfunction or disruptions in their daily activities, they were excluded. The University of Minnesota institutional review board approved this study and all associated protocols. Subjects completed the behavioral portion during one visit and then returned for an additional MRI session. All participants provided written informed consent at the beginning of every visit.

Measures

Personality questionnaires. All participants in the study sample completed the Big Five Inventory (BFI) and the Big Five Aspects Scales (BFAS). The BFI consists of 44 items across the broad Big Five traits (Neuroticism, Agreeableness, Conscientiousness, Openness/Intellect, and Extraversion) and has been used widely across many samples (John, Donahue, & Kentle,1991; John, Naumann, & Soto, 2008). The BFAS is a personality inventory that measures the two major subfactors within each of the Big Five (called “aspects”) (DeYoung, Quilty, & Peterson, 2007). Additionally, approximately 65% of the sample had at least 2 peer ratings using peer-report versions of the BFI and BFAS and 70% of the sample had at least 1 peer rating. Peer ratings were

obtained by giving participants 3 informant packets that included a stamped and pre-addressed envelope. The BFI and BFAS were combined for a composite Conscientiousness score, including both self- and peer-ratings of Conscientiousness when those were available. Males scored significantly lower (M = 3.453, SD = 0.520) than females (M = 3.660, SD = 0.436) on Conscientiousness (t_{216} = 3.203, p = .002), which is in line with previous research (Schmitt, Realo, Voracek, & Allik, 2008).

Intelligence. All participants in the study sample completed the Wechsler Adult Intelligence Scale – Fourth Edition (WAIS-IV). Full scale IQ was estimated based on a validated, 4-test composite score from the WAIS-IV (Wechsler, 2008). The subtests used in the composite scores were: Block Design, Matrix Reasoning, Vocabulary, and Similarities. Consistent with previous findings, there was a significant negative relation between IQ and Conscientiousness (r = -.18, p < .001). IQ was included as a covariate in the analysis because of this slight negative correlation and its well-established associations with brain function (Higgins et al., 2007; Luciano et al., 2006).

Image Acquisition and Pre-Processing

Resting state functional MRI scans were acquired using a 3T Siemens Trio scanner (Erlangen, Germany) at the University of Minnesota's Center for Magnetic Resonance Research. Participants were instructed to stay awake during the scan and to gaze at a basic fixation cross projected on a screen inside the bore. Subjects were instructed to click a button when the fixation cross changed from gray to white, or vise versa, which occurred five times during each resting state scan. This protocol ensured that the subjects remained awake while minimizing eye movements for the entire

duration of the scan. Other researchers have successfully used protocols similar to this one (Fair et al., 2007; Fox et al., 2009; Fox and Grecius, 2009). Scan sequence parameters were as follows: gradient-echo echo-planar imaging of 150 volumes; repetition time (TR) = 2s; echo time (TE) = 28 ms; flip angle = 80°; voxel size = 3.5 x 3.5 x 3.5 mm. A high-resolution T1-weighted MPRAGE was collected for registration purposes. Pre-processing followed the standard protocol using FMRIB Software Library (FSL 4.1.9), which included: brain extraction, motion correction, intensity normalization of the 4D data, spatial smoothing, high pass temporal filtering, and registration of 4D data to high resolution T1-weighted structural images. Head motion during the scans was accounted for with motion parameter regression.

Independent Components Analysis

ICNs were created using a meta-ICA pipeline in FSL (see Poppe et al., 2013 and Abram et al., 2015 for more details). Sixty components were extracted. Artifactual components were identified per Kelly and colleague's (2010) recommendations, and a final set of 27 non-artifactual components was retained for further investigation.

Network Coherence Calculations

Each of the 27 group-level spatial masks was used as a spatial regressor on each individual's resting state fMRI scan to give us two main parameters of interest, functional coherence within ICNs and functional connectivity between ICNs (Abram et al., 2015). The group-level spatial mask regressors provided subject-specific time series for each mask (i.e. each subject had time series values for all voxels within each of the 27 masks). These subject-specific time series were used to create mask-specific average temporal

maps for each subject. Then, the value of each voxel in the subject-specific timeseries was compared to the mask-specific average temporal maps for each of the 27 masks for each subject. This value, the first parameter of interest, represents how well the overall ICN temporal activation corresponds to the specific voxel timeseries' for each component (i.e., it represents the overall coherence within each ICN by subject). Larger values reflect higher overall coherence of a component. These values are subject-specific, and thus, there are individual differences in them. The second parameter of interest, functional connectivity between ICNs, was calculated by correlating the timeseries of two ICNs' to assess the synchrony of pairs of ICNs within each subject. For more details regarding the derivation of network coherence calculations, see Abram et. al. (2015).

Goal Priority Network Components

Components that appeared similar to previous brain regions in the GPN by Yeo et al. (2011) were identified using visual inspection. The components in our sample are likely implicated in motivational, goal-oriented behavior given their overlap with previously specified ventral attention or salience networks. To visually compare our networks with Yeo et al. (2011) networks, we obtained Buckner's 7 network parcellation mask (https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation_Yeo2011) and extracted each of the 7 networks into separate masks using FreeSurfer (http://freesurfer.net/). After separating the 7 networks we used AFNI (Analysis of Functional NeuroImages; https://afni.nimh.nih.gov/afni) to reorient and change the resolution of the 7-network parcellation maps to match the orientation and resolution (2mm) of our extracted ICN maps (Cox, 1996).

Visual inspection was conducted using FSLView (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FslView/) indicated four ICNs that appeared to correspond to regions of the GPN, with regions characterized as follows: (ICN-1) regions of the dorsal anterior cingulate cortex (dACC) and regions of the insula, (ICN-2) parts of the LPFC, parts of the dorsomedial prefrontal cortex (dmPFC) and insula, (ICN-3) regions in the LPFC, dACC, and temporoparietal junction (TPJ), and (ICN-4) regions in the rIFG and TPJ (see Figure 1 for these ICNs and Figure 2 for their overlap with the GPN as depicted by Yeo et al. (2011)). Five networks were retained and hypothesized to overlap with Yeo and colleagues (2011) DN (ICNs 8 -12), and three networks were retained and hypothesized to overlap with their FPCN (ICNs 5-7).

Results

Goal Priority Network Coherence Analyses

First, a partial correlation analysis was conducted examining the relation of the four GPN networks to Conscientiousness while controlling for age, sex, IQ, and the eight other networks (DN and FPCN). One of the four proposed GPN networks remained significantly correlated with Conscientiousness after correcting for multiple comparisons. Table 1 presents partial correlations between Conscientiousness and each of the components of the proposed GPN ICNs. The dACC and insula component (ICN-1) was significantly correlated with Conscientiousness (r = .212, p = .002). The rest of the non-significant findings and zero-order correlations can be found in Table 1. GPN components were also compared to all of the other Big Five traits (Openness, Extraversion, Neuroticism, and Agreeableness). None of the components showed

significant correlations with any of the other Big Five measures when controlling for age, sex, IQ, the 5 DN components, and the 3 FPCN components, suggesting that these proposed networks are specific to Conscientiousness (see Table 2).

To show discriminant validity, Table 1 also displays results for partial correlations between Conscientiousness and each of the components for both the FPCN and DN. There were no significant relationships between Conscientiousness and FPCNs. Out of the 5 DN components, two were significantly negatively correlated with Conscientiousness, but were not significant after correcting for multiple comparisons. The ICNs trending towards being negatively correlated with Conscientiousness included the superior temporal gyrus and the temporal parietal junction (ICN-8, DN), and the dorsomedial prefrontal cortex (ICN-12, DN).

Goal Priority Network Connectivity Analyses

Because the GPN has four components, we calculated zero-order correlations and partial correlations to investigate the relations between six possible interconnectivity values and Conscientiousness scores while controlling for age, sex, and IQ. Table 3 displays results for the correlations between Conscientiousness and between-component connectivity.

The correlations between Conscientiousness and connectivity between the dACC/insula component (ICN-1, GPN) and all the other GPN components were significant, but only the connectivity between the dACC/insula component (ICN-1, GPN) and the LPFC/dACC/TPJ component (ICN-3, GPN) remains significant after accounting for multiple comparisons. All of the Conscientiousness connectivity results can be found

in Table 3. These results suggest that higher connectivity between the dACC/insula ICN (ICN-1, GPN) and the other networks in the GPN is associated with higher Conscientiousness. The connectivity between the rIFG/TPJ component (ICN-4, GPN) and the dmPFC/insula/LPFC component (ICN-2, GPN) was significantly negatively correlated with Conscientiousness (r = -.151, p < .05), indicating that as these two components are less related, Conscientiousness scores increase. However, this result does not stay significant when correcting for multiple comparisons.

To conduct a sensitivity analysis, we compared connectivity values among both the FPCN components and the DN components to Conscientiousness by obtaining partial correlations controlling for age, sex, and IQ. None of the FPCN connectivity values were significantly correlated with Conscientiousness scores, even though one of the three FPCNs overlapped substantially with Yeo and colleagues (2011) GPN. Of the connectivity values associated with the DN components, only one connectivity value showed a significant correlation with Conscientiousness. The connectivity between the precuneus/angular gyrus component (ICN-10, DN) and the superior temporal gyrus/temporalparietal junction component (ICN-8, DN) was significantly correlated with Conscientiousness (r = -.136, p = .047), but this correlation does not remain significant after correcting for multiple comparisons.

To show discriminant validity, we conducted additional partial and zero-order correlation analyses comparing Neuroticism, Agreeableness, Extraversion, and Openness scores with the six GPN connectivity values (see Table 4). None of the other Big Five traits yielded similar correlations between connectivity values and Conscientiousness;

however, Neuroticism was significantly negatively correlated with connectivity values between with the dACC/Insula (ICN-1, GPN) component and the dmPFC/insula/LPFC (ICN-2, GPN) component. Because this connectivity is within the insula, and insula function is associated with anxiety, negative affect, and Neuroticism (Markett et al., 2013; Wu, Samanez-Larkin, Katovich, & Knutson, 2014), it is plausible that lower connectivity involving insula ICNs would be associated with higher trait Neuroticism.

Exploratory Analyses

Exploratory connectivity analyses were conducted to see if the connectivity between any of the GPN components and any FPCNs and DNs were related to Conscientiousness. Of the 32 connectivity values, only two were related to Conscientiousness at $p < .05$ uncorrected. Connectivity between the insula/dACC (ICN-1, GPN) component and the superior temporal gyrus/temporalparietal junction (ICN-8, DN) component was significantly correlated with Conscientiousness ($r = .139$, $p = .042$) when controlling for age, sex, and IQ. While this does not remain significant after correcting for multiple comparisons, this trend is not surprising given the ICN-8 (DN) was significantly correlated with Conscientiousness in all previous analyses and also had the highest overlap of all of the DN components with Yeo and colleagues' (2011) VAN. Connectivity between the LPFC/dACC/TPJ (ICN-3, GPN) component and the DLPFC/frontal pole (ICN-7, FPCN) component was significantly correlated with Conscientiousness ($r = -.137$, $p = .045$) when controlling for age, sex, and IQ, but does not remain significant after correcting for multiple comparisons.

Discussion

Supporting our hypothesis, one of the four GPN ICNs in the analysis showed significant correlations with Conscientiousness. The coherence of the dACC/Insula component (ICN-1, GPN) was positively related to Conscientiousness, which suggests that the more synchrony that exists in this small network comprising regions of dACC and insula, the higher the Conscientiousness score. Additionally, interconnectivity between the dACC/insula component (ICN-1, GPN) and the rest of the GPN was positively associated with Conscientiousness as well. This suggests that a more synchronously activated GPN is associated with higher Conscientiousness scores. Coherence in the other three GPN ICNs did not show significant correlations with Conscientiousness, suggesting that the dACC/insula component and its connection to the rest of the GPN may be particularly important for the maintenance of motivational stability and nonimmediate goal attainment.

These results seem to be in line with previous research. As previously mentioned, Adelstein and colleagues (2011) found that higher coherence in the ACC is related to higher trait Conscientiousness. Menon and Uddin (2010) reported that the insula is intricately involved in cognitive control and attentional processes and that the anterior insula and ACC form a "salience network" that guides behavior towards relevant stimuli and away from distractions. These findings were reported in both disordered and neurotypical adults. This is consistent with our results and suggests that we are finding similar, but potentially more broadly defined, regions involved in the regulation of motivation. The dACC/insula component (ICN-1, GPN) may be what is typically called the "salience network" but it is clear that it is functionally connected to many other

regions implicated in the GPN and that all of these components, in concert, contribute to Conscientiousness.

When assessing the interconnectivity between the rIFG/TPJ (ICN-4, GPN) component and the dmPFC/insula/LPFC (ICN-2, GPN) component, we found a significantly negative correlation with Conscientiousness. This pattern suggests, as these two components are less related, Conscientiousness scores increase. This may imply that the main hub of the GPN is this dACC/insula component (ICN-1, GPN) and that this component is the first source of motivational goal attainment and focus on long-term goals. It may be beneficial to study these regions using a lag analysis in the future to get a better idea of how these regions interact temporally.

It is important to note that our proposed GPNs do overlap with other networks in Yeo and colleagues (2011) 7-network parcellation, but that these overlaps are to be expected because our networks are not exclusive (i.e., one voxel can be part of multiple ICNs). For example, our GPNs overlap with Yeo and colleague's FPCN to some extent, but not to the same extent as with their VAN. Previous research by D'Esposito and colleagues (1995) supports the notion that frontal control networks may occupy similar areas as attentional networks in the brain. Our networks may differ from Yeo and colleagues' (2011) networks because their methods created networks that were spatially exclusive and we chose not add that constraint to our analysis, given the use of ICA. Additionally, our dmPFC/insula/LPFC GPN component (ICN - 2) overlapped most with their FPCN where it extended into the LPFC and dmPFC, which has been implicated in IQ and working memory tasks. As previously addressed, these tasks are slightly

negatively correlated with Conscientiousness, and thus, we would hypothesize that the coherence of the dmPFC/insula/LPFC component (ICN-2) may show correlations near zero since it shares space with both FPCN and GPN neural activities.

The developmental relation between a trait and its neural substrate is inevitably somewhat ambiguous, given the relation to previous behaviors of the individual. Conscientiousness is positively associated with beneficial health-related behavior and negatively associated with risky behaviors, such as drug use, which may impact neural structure and function (Jackson, Balota, & Head, 2011, Ozer & Benet-Martínez, 2006). To disentangle the causal relations of traits and brain function, it will be necessary to conduct longitudinal studies in the future.

Conclusion

The current study successfully found associations between a functional neural network and Conscientiousness. Results suggest that Conscientiousness is related to a broad motivational attention network that comprises both the salience and VAN, which we labeled the goal priority network. Coherence within GPN networks was positively associated with higher trait Conscientiousness, and higher connectivity between two of the GPN networks was also associated with higher Conscientiousness. These results provide support for the hypothesis that the GPN is an important neural substrate of Conscientiousness (Allen & DeYoung, 2016; DeYoung, 2015).

If we are able to understand why people are able to inhibit impulses or direct their attention towards nonimmediate goals, it may be possible to better treat people with impulse-control disorders or help underachieving youth. Functional connectivity is

malleable through experience (functional connectivity changes over the course of development) as well as through psychopharmacological treatment (Vaidya & Gordon, 2013). The flexibility of the human brain is immense. It may be possible to make these networks more efficient via coursework or treatments, which has the potential to make life better and more satisfying for people who suffer from low levels of Conscientiousness.

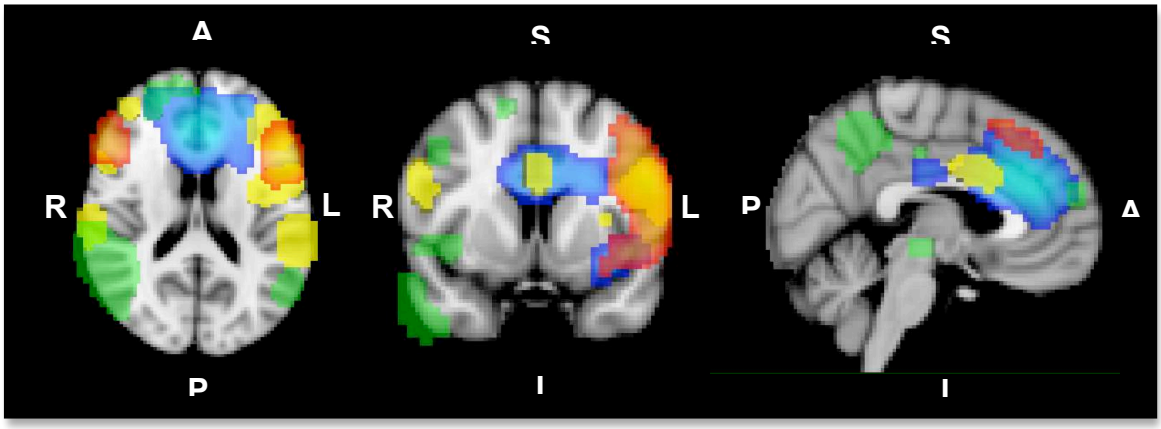

Figure 1. Proposed GPN intrinsic connectivity networks (ICNs): (1) dACC and insula (blue), (2) dmPFC, LPFC and insula (red), (3) LPFC, dACC, and TPJ (yellow), and (4) rIFG and TPJ (green)

dACC = dorsal anterior cingulate cortex, dmPFC = dorsomedial prefrontal cortex, LPFC = lateral prefrontal cortex, TPJ = temporoparietal junction, rIFG = right inferior frontal gyrus

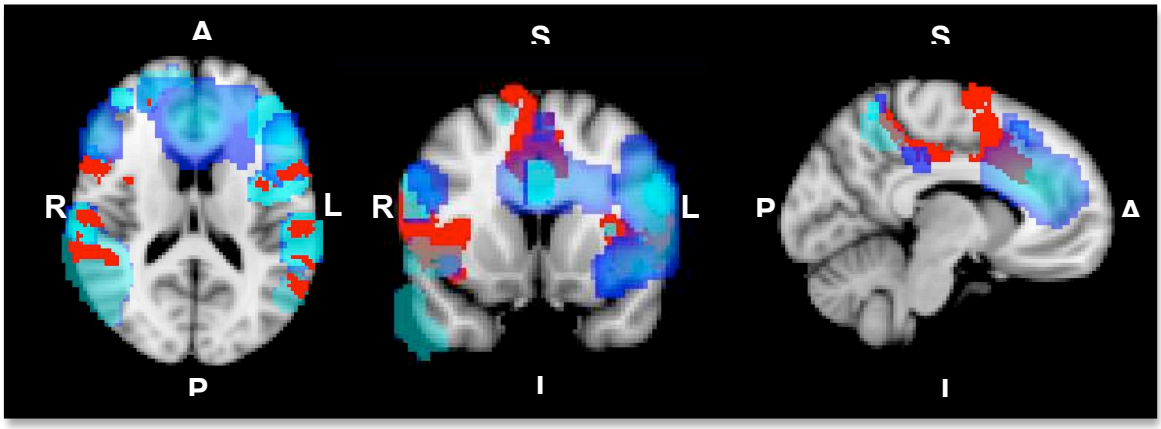

Figure 2. Proposed GPN intrinsic connectivity networks (ICNs) compared to Yeo and colleague's (2011) VAN. Our GPN: Blue. Yeo and colleague's (2011) VAN: Red.

Table 1. Partial Correlations of Goal Priority Network, Frontoparietal Control Network, and Default Network Component Coherence and Conscientiousness. (N = 218). Partial correlations controlling for age, sex, IQ, and components in other networks (e.g. when testing a GPN component, we controlled for all FPCN and DN components). Zero-order correlations in parentheses.

GPN Component	Conscientiousness
(1) dACC & Insula	**.212**** (.067)
(2) dmPFC, Insula, LPFC	-.029 (-.097)
(3) LPFC, dACC, TPJ	.055 (-.028)
(4) rIFG, TPJ	.079 (.006)
FPCN Component	
(5) rFPCN	.058 (-.025)
(6) lFPCN	.060 (.019)
(7) DLPFC/frontal pole	-.024 (-.067)
DN Component	
(8) STG/TJP	-*.145** (-.127)
(9) Precuneus	.003 (.018)
(10) Precuneus/angular gyrus	-.021 (.033)
(11) mPFC	-.081 (-.064)
(12) dmPFC	-*.144** (-.115)

**** p < .01**
** p < .05*

dACC = dorsal anterior cingulate cortex, dmPFC = dorsomedial prefrontal cortex, LPFC = lateral prefrontal cortex, TPJ = temporoparietal junction, rIFG = right inferior frontal gyrus, rFPCN = right fronto-parietal control network, lFPCN = left fronto-parietal control network, DLPFC = dorsolateral prefrontal cortex, STG = superior temporal gyrus, mPFC = medial prefrontal cortex

Table 2. Partial and zero-order correlations between N, A, E, and O and GPN, partial above the diagonal, zero-order below the diagonal, means (sds) on the diagonal. P-values are in the parentheses. Partial Correlations controlling for sex, age, 8 other components (DNs and FPCNs), and IQ.

	N	A	E	O	(1)	(3)	(4)	(2)
N	2.613 (.644)	**-.485(.000)**	**-.347(.000)**	.056 (.421)	-.133 (.057)	.001 (.987)	.011 (.871)	-.037 (.596)
A	**-.433 (.000)**	3.955(.463)	**.213 (.002)**	.101 (.146)	.101 (.146)	.001 (.993)	-.081 (.248)	.053 (.445)
E	**-.350 (.000)**	**.199 (.003)**	3.508(.617)	.127 (.067)	.064 (.357)	.135 (.053)	.076 (.274)	-.050 (.473)
O	-.023 (.733)	.034 (.617)	.121 (.074)	3.903(.451)	.077 (.269)	-.039 (.572)	-.047 (.501)	.044 (.533)
(1) Insula/dACC	-.111 (.102)	.025 (.719)	**.185 (.006)**	.131 (.054)	13.174 (3.824)	-.066 (.345)	.070 (.314)	**.230 (.001)**
(3) TPJ/LPFC/ACC	-.098 (.151)	-.044(.517)	**.247 (.000)**	*.153 (.024)*	**.443 (.000)**	16.334 (4.377)	**.272 (.000)**	.107 (.126)
(4) rIFG/TPJ	-.092 (.178)	-.107(.114)	**.206 (.002)**	*.141 (.038)*	**.437 (.000)**	**.645 (.000)**	10.049(2.606)	-.061 (.384)
(2) dmPFC/Insula/LPFC	-.062 (.363)	-.005(.936)	.112 (.099)	*.138 (.041)*	**.639 (.000)**	**.551 (.000)**	**.400 (.000)**	19.649 (4.764)

dACC = dorsal anterior cingulate cortex, dmPFC = dorsomedial prefrontal cortex, LPFC = lateral prefrontal cortex, TPJ = temporoparietal junction, rIFG = right inferior frontal gyrus

Table 3. Partial correlations of GPN Interconnectivity and Conscientiousness controlling for age, sex, and IQ. Zero order correlations in parentheses (N = 218).

GPN Component 1	GPN Component 2	Conscientiousness
dACC /Insula (1)	LPFC/dACC/TPJ (3)	*.174** **(.200**)**
dACC/Insula (1)	rIFG/TPJ (4)	*.153** (.107)
dACC/Insula (1)	dmPFC/Insula/LPFC (2)	*.169* (.160*)*
LPFC/dACC/TPJ (3)	rIFG/TPJ (4)	-.033 (-.038)
LPFC/dACC/TPJ (3)	dmPFC/Insula/LPFC (2)	-.051 (-.036)
rIFG/TPJ (4)	dmPFC/Insula/LPFC (2)	*-.151* (-.153*)*

**** p < .01**
** p < .05*

dACC = dorsal anterior cingulate cortex, LPFC = lateral prefrontal cortex, TPJ = temporoparietal junction, rIFG = right inferior frontal gyrus, dmPFC = dorsomedial prefrontal cortex

Table 4. Partial correlations of GPN Interconnectivity and N, A, E, and O. Zero-order correlations in parentheses (N = 218).

GPN Component 1	GPN Component 2	N	A	E	O
dACC /Insula (1)	LPFC/dACC/TPJ (3)	*-.150** (-.130)	.085 (.106)	.061 (.067)	.010 (-.043)
dACC/Insula (1)	rIFG/TPJ (4)	*-.151* (-.166*)*	.029 (.000)	-.035 (-.027)	-.078 (-.017)
dACC/Insula (1)	dmPFC/Insula/LPFC (2)	**-.190** (-.194**)**	*.146** (.128)	.091 (.092)	.056 (.030)
LPFC/dACC/TPJ (3)	rIFG/TPJ (4)	-.074 (-.078)	.024 (.022)	.070 (.049)	.079 (.081)
LPFC/dACC/TPJ (3)	dmPFC/Insula/LPFC (2)	-.072 (-.072)	.061 (.058)	.021 (.032)	-.033 (-.074)
rIFG/TPJ (4)	dmPFC/Insula /LPFC (2)	-.038()	-.003 (-.022)	.016(.023)	.063 (.081)

**** p < .01**

** p < .05*

dACC = dorsal anterior cingulate cortex, LPFC = lateral prefrontal cortex, TPJ = temporoparietal junction, rIFG = right inferior frontal gyrus, dmPFC = dorsomedial prefrontal cortex, N = Neuroticism, A = Agreeableness, E = Extraversion, O = Openness

Table 5. Means and standard deviations of all measures. (N = 218)

Measure	Mean	SD
Conscientiousness	3.559	0.489
Openness	3.903	0.451
Extraversion	3.508	0.617
Agreeableness	3.955	0.463
Neuroticism	2.613	0.644
(1, GPN) Insula/ACC	13.174	3.824
(3, GPN) LPFC/ACC/TPJ	16.334	4.377
(4, GPN) rIFG/TPJ	10.049	2.606
(2, GPN) dmPFC/Insula/LPFC	19.649	4.764
(5, FPCN) rFPCN	21.794	5.006
(6, FPCN) lFPCN	21.737	5.379
(7, FPCN) DLPFC/frontal pole	15.796	4.740
(8, DN) STG/TJP	14.616	4.722
(9, DN) Precuneus	31.051	8.351
(10, DN) Precuneus/Angular Gyrus	19.444	4.174
(11, DN) mPFC	30.084	8.933
(12, DN) dmPFC	26.347	7.521
Age	25.771	4.556
IQ	115	15.64

dACC = dorsal anterior cingulate cortex, LPFC = lateral prefrontal cortex, TPJ = temporoparietal junction, rIFG = right inferior frontal gyrus, STG = superior temporal gyrus, mPFC = medial prefrontal cortex, dmPFC = dorsomedial prefrontal cortex, rFPCN = right fronto-parietal control network, lFPCN = left fronto-parietal control network, DLPFC = dorsolateral prefrontal cortex

Table 6. Zero-order correlations between all networks and the Big 5.

	O	C	E	A	N	(1)	(3)	(4)	(2)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
Openness	**1**	**-.208 (.002)**	.121 (.074)	.034 (.617)	-.023 (.733)	.131 (.054)	*.153 (.024)*	*.141 (.038)*	*.138 (.041)*	*.169 (.012)*	**.205 (.002)**	*.152 (.024)*	*.160 (.018)*	*.151 (.026)*	*.133 (.050)*	-.018 (.792)	.119 (.079)
Conscientiousness		**1**	**.294 (.000)**	**.327 (.000)**	**-.466 (.000)**	.067 (.328)	-.028 (.682)	.006 (.935)	-.097 (.154)	-.025 (.709)	.019 (.775)	-.067 (.323)	-.127 (.060)	.018 (.788)	.033 (.627)	-.064 (.349)	-.115 (.090)
Extraversion			**1**	**.199 (.003)**	**-.350 (.000)**	**.185 (.006)**	**.247 (.000)**	**.206 (.002)**	.112 (.099)	.110 (.104)	**.204 (.002)**	*.142 (.037)*	*.152 (.024)*	*.150 (.027)*	**.230 (.001)**	.132 (.051)	.123 (.070)
Agreeableness				**1**	**-.433 (.000)**	.025 (.719)	-.044 (.517)	-.092 (.178)	-.062 (.363)	-.048 (.481)	-.054 (.428)	-.028 (.682)	.009 (.897)	.037 (.591)	.053 (.439)	-.047 (.492)	*-.149 (.027)*
Neuroticism					**1**	-.111 (.102)	-.098 (.151)	-.092 (.178)	-.062 (.363)	-.094 (.169)	-.090 (.187)	-.052 (.442)	-.062 (.361)	-.118 (.083)	-.132 (.052)	.026 (.705)	-.022 (.749)
(1, GPN) Insula/ACC						**1**	**.443 (.000)**	**.437 (.000)**	**.639 (.000)**	**.461 (.000)**	**.379 (.000)**	**.666 (.000)**	**.473 (.000)**	**.292 (.000)**	**.370 (.000)**	**.631 (.000)**	**.614 (.000)**
(3, GPN) LPFC/ACC/TPJ							**1**	**.645 (.000)**	**.551 (.000)**	**.620 (.000)**	**.528 (.000)**	**.527 (.000)**	**.527 (.000)**	**.472 (.000)**	**.477 (.000)**	**.439 (.000)**	**.468 (.000)**
(4, GPN) rIFG/TPJ								**1**	**.400 (.000)**	**.560 (.000)**	**.521 (.000)**	**.441 (.000)**	**.430 (.000)**	**.459 (.000)**	**.447 (.000)**	**.343 (.000)**	**.451 (.000)**
(2, GPN) dmPFC/Insula/LPFC									**1**	**.550 (.000)**	**.435 (.000)**	**.653 (.000)**	**.555 (.000)**	**.276 (.000)**	**.298 (.000)**	**.559 (.000)**	**.534 (.000)**
(5, FPCN) rFPCN										**1**	**.588 (.000)**	**.598 (.000)**	**.398 (.000)**	**.346 (.000)**	**.334 (.000)**	**.430 (.000)**	**.495 (.000)**
(6, FPCN) lFPCN											**1**	**.462 (.000)**	**.339 (.000)**	**.444 (.000)**	**.390 (.000)**	**.283 (.000)**	**.401 (.000)**
(7, FPCN) DLPFC/frontal pole												**1**	**.458 (.000)**	**.300 (.000)**	**.294 (.000)**	**.576 (.000)**	**.663 (.000)**
(8, DN) STG/TJP													**1**	**.466 (.000)**	**.434 (.000)**	**.420 (.000)**	**.303 (.000)**
(9, DN) Precuneus														**1**	**.526 (.000)**	**.212 (.002)**	***.165 (.015)***
(10, DN) Precuneus/Angular Gyrus															**1**	**.358 (.000)**	**.211 (.002)**
(11, DN) mPFC																**1**	**.582 (.000)**
(12, DN) dmPFC																	**1**

dACC = dorsal anterior cingulate cortex, LPFC = lateral prefrontal cortex, TPJ = temporoparietal junction, rIFG = right inferior frontal gyrus, STG = superior temporal gyrus, mPFC = medial prefrontal cortex, dmPFC = dorsomedial prefrontal cortex, rFPCN = right fronto-parietal control network, lFPCN = left fronto-parietal control network, DLPFC = dorsolateral prefrontal cortex

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